

Diapause in Various Populations of *Pieris napi* L. from Different Parts of the British Isles

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Diapause has been defined (Beck, 1967) as a genetically determined state of suppressed development, the manifestation of which may be induced by environmental factors. It follows, therefore, that different, geographically isolated populations of a butterfly should have different assemblages of genes determining diapause and hence should show a somewhat different diapause response to the same environmental conditions. The phase of development in which *Pieris napi* L. undergoes diapause is the pupal phase. Whether or not an individual undergoes pupal diapause depends in part on the photoperiod and temperature encountered during late larval life (Danilevskii, 1961). This, in turn, determines whether a particular population of the species is monovoltine or polyvoltine. *P. napi* is usually regarded as being partially bivoltine in the British Isles (Lees and Archer, 1974), but this statement hardly does justice to the complex situation which prevails over the country as a whole.

Colonies of *P. napi* which are strictly monovoltine are known (Lees, 1970) and these are usually found at altitudes of 800 feet or more in Northern England and Scotland. Elsewhere in the British Isles the species is at least partially bivoltine or even partially trivoltine. It should be noted, however, that even in those parts of the country where there is a second and third brood, a significant part of the pupae derived from the spring generation are diapause pupae and do not develop into butterflies until the following year.

In order to learn more of the diapause characteristics of *Pieris napi* in different parts of the British Isles, we sampled spring populations of the species from various localities ranging from Teignmouth in S. Devon to Dollar in Scotland, although the majority of samples were from populations in N. England (c.f. Fig. 1). Eggs from the captured females were kept in plastic boxes until they hatched and the resultant larvae were maintained under controlled conditions of photoperiod and temperature until they pupated. The larvae were fed on the leaves of Hedge Garlic (*Alliaria petiolata*), a common foodplant of this species in the field.

The photoperiod chosen for the experiments was 18 hours, which is a "long-day" photoperiod, similar to the daylength of the longest day over much of England. The larvae were reared at two temperatures viz. 18 degrees C and 12 degrees C. The former is similar to the mean maximum of the warmest month in S. England, the latter is similar to the mean maximum of the warmest month at altitudes of 1000 feet in N. England and Scotland. The numbers and percentages of diapause and non-diapause pupae obtained in the various experiments are shown in Tables 1 and 2.

Table 1
Experiments at 18 Hr. Photoperiod and 18 Degrees C

Locality	Elevation (M.)	Offspring of Female	No. of Diapause Pupae Produced Among Progeny	No. of Non-Diapause Pupae Produced Among Progeny
Dollar	48	1	5 (19.2%)	21 (80.8%)
Dollar	48	2	6 (16.6%)	30 (83.4%)
Dollar	48	3	8 (23.5%)	26 (76.5%)
Dollar	48	4	6 (14.0%)	42 (86.0%)
Bellingham	122	1	8 (16.6%)	40 (83.4%)
Bellingham	122	2	6 (14.3%)	36 (85.7%)
Bellingham	122	3	6 (8.7%)	39 (91.3%)
Bellingham	122	4	4 (18.2%)	18 (81.8%)
High Force	381	1	7 (15.5%)	38 (84.5%)
High Force	381	2	8 (16.6%)	40 (83.4%)
High Force	381	3	9 (20.9%)	36 (79.1%)
High Force	381	4	4 (16.0%)	21 (84.0%)
Arnside	15	1	6 (17.6%)	38 (82.4%)
Arnside	15	2	2 (6.9%)	27 (93.1%)
Arnside	15	3	3 (10.4%)	25 (89.6%)
Strensall	15	1	6 (14.3%)	36 (85.7%)
Strensall	15	2	3 (10.8%)	25 (89.2%)
Strensall	15	3	4 (11.8%)	30 (88.2%)
Strensall	15	4	2 (6.6%)	28 (93.4%)
Menston	48	1	3 (13.1%)	20 (86.9%)
Menston	48	2	2 (7.3%)	25 (92.7%)
Menston	48	3	2 (8.7%)	23 (91.3%)
Menston	48	4	4 (11.8%)	30 (88.2%)
Nantwich	30	1	2 (8.7%)	22 (91.3%)
Nantwich	30	2	1 (4.0%)	24 (96.0%)
Nantwich	30	3	3 (7.9%)	36 (92.1%)
Teignmouth	8	1	2 (6.7%)	28 (93.3%)
Teignmouth	8	2	4 (11.8%)	30 (88.2%)
Teignmouth	8	3	3 (7.7%)	36 (92.3%)
Teignmouth	8	4	2 (6.4%)	29 (93.6%)

Table 2
Experiments at 18 Hr. Photoperiod and 12 Degrees C

Locality	Elevation (M.)	Offspring of Female	No. of Diapause Pupae Produced Among Progeny	No. of Non-Diapause Pupae Produced Among Progeny
Dollar	48	1	31 (100%)	0 (0.0%)
Dollar	48	2	43 (100%)	0 (0.0%)
Dollar	48	3	19 (100%)	0 (0.0%)
Dollar	48	4	25 (100%)	0 (0.0%)
Bellingham	122	1	23 (100%)	0 (0.0%)
Bellingham	122	2	37 (100%)	0 (0.0%)
Bellingham	122	3	24 (100%)	0 (0.0%)
Bellingham	122	4	36 (100%)	0 (0.0%)
High Force	381	1	20 (100%)	0 (0.0%)
High Force	381	2	34 (100%)	0 (0.0%)
High Force	381	3	31 (100%)	0 (0.0%)
High Force	381	4	28 (100%)	0 (0.0%)
Arnside	15	1	24 (88.8%)	3 (11.2%)
Arnside	15	2	48 (85.7%)	8 (14.3%)
Arnside	15	3	30 (83.3%)	6 (16.7%)
Arnside	15	4	20 (77.0%)	6 (23.0%)
Strensall	15	1	21 (91.3%)	2 (8.7%)
Strensall	15	2	27 (90.0%)	3 (10.0%)
Strensall	15	3	50 (89.4%)	6 (10.6%)
Menston	48	1	22 (84.6%)	4 (15.4%)
Menston	48	2	40 (85.1%)	7 (14.9%)
Menston	48	3	42 (89.4%)	5 (10.6%)
Nantwich	30	1	20 (80.0%)	5 (20.0%)
Nantwich	30	2	37 (83.4%)	7 (16.6%)
Nantwich	30	3	39 (81.4%)	8 (18.6%)
Teignmouth	8	1	29 (82.9%)	6 (17.1%)
Teignmouth	8	2	39 (79.6%)	10 (20.4%)
Teignmouth	8	3	32 (80.0%)	8 (20.0%)
Teignmouth	8	4	21 (81.5%)	5 (18.5%)

From the results given in Table 1 it is obvious that larvae from all localities, maintained at a temperature of 18 degrees C and 18 hrs photoperiod, produced some pupae which were diapause and some which were non-diapause. In all cases the numbers of non-diapause pupae greatly exceeded the numbers of diapause pupae, but the percentages of non-diapause pupae were highest in the population from S. England (Teignmouth) and from localities in N. England at low altitudes. It is reasonable to infer that at a temperature of 18 degrees C, populations of *P. napi* would be overwhelmingly bivoltine, although in all the localities we

have sampled at least some genotypes for monovoltinism are present. This temperature is above the mean temperature of the warmest month in any part of the British Isles, so that populations in nature are likely to be somewhat less bivoltine than the experimental data suggests.

The results in Table 2 indicate that larvae maintained at the lower temperature of 12 degrees C behave very differently from those at 18 degrees C, in the extent to which they yield diapause pupae. Larvae from three localities (High Force, Bellingham and Dollar) gave no non-diapause pupae under these conditions and those from other localities did not give more than 20% non-diapause pupae. Once again the percentages of non-diapause pupae were highest in the population from S. England (Teignmouth), and the populations which behave in a strictly monovoltine fashion are those from high altitudes in N. England and from Scotland. The experimental data is therefore in agreement with what is observed in nature viz. the occurrence of monovoltine colonies in localities where the summer temperatures are low.

Our findings suggest that populations of *P. napi* show a physiological cline in relation to the tendency of their larvae to give diapause pupae as one moves from north to south in the British Isles. Northern populations are more prone to give diapause pupae than southern ones and there is a well-defined gradient with extremes at Dollar in Scotland and Teignmouth in S. England. This physiological cline is accompanied by a phenotypic gradient. The female butterflies from Scotland and the extreme north of England have much darker veining to the wings and a proportion of them have a ground colour which is some shade of yellow instead of white. These tendencies, which are more marked in the spring brood, become progressively less evident as one moves from north to south. Warren (1968) has suggested that the northern forms of *P. napi* should be regarded as forming a distinct subspecies *P. napi thomsoni* Warren, and Thomson (1970) has described the distribution of the latter. It is obvious from Thomson's account that the phenotypes he describes constitute a cline.

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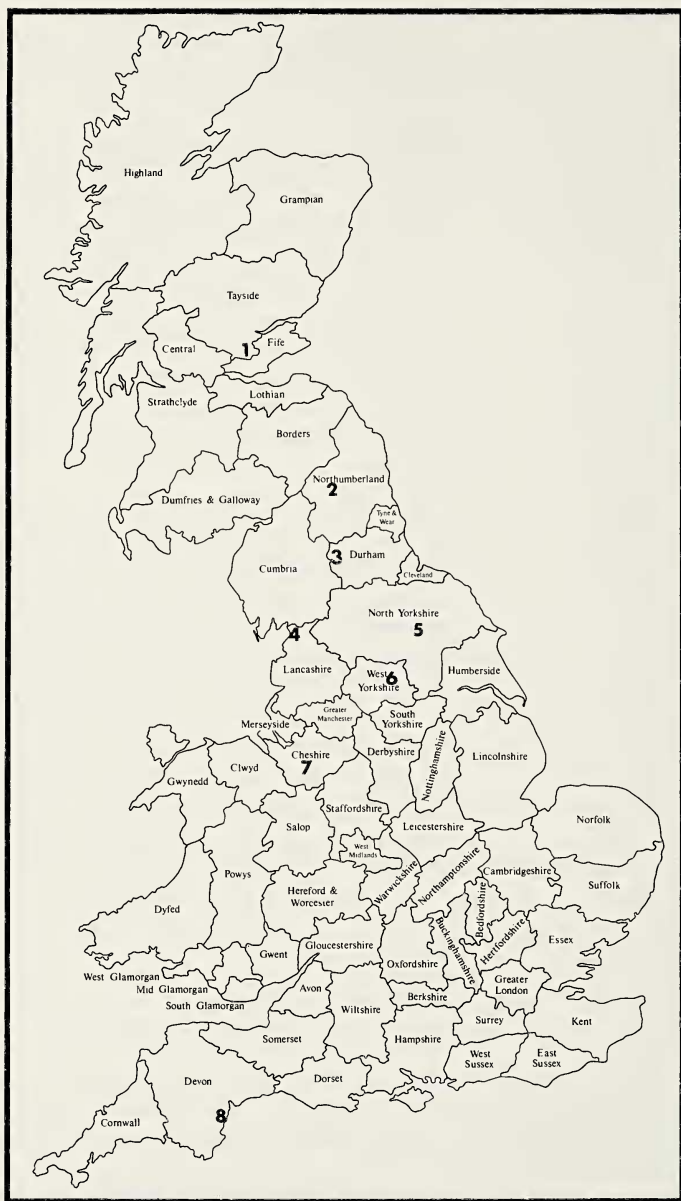


Fig. 1. Locations of sampled *P. napi* populations.

1 - Dollar; 2 - Bellingham; 3 - High Force; 4 - Arnside; 5 - Strensall; 6 - Menston; 7 - Nantwich; 8 - Teignmouth.